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THE PRESCOTT SCALE (MATSUCOCCUS VEXILLORUM) AND ASSOCIATED ORGANISMS THAT CAUSE FLAGGING INJURY TO PONDEROSA PINE IN THE SOUTHWEST[1]

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INTRODUCTION

In 1918 a so-called twig blight of young ponderosa pine (*Pinus ponderosa* Laws.) was noted in the Prescott National Forest, in Arizona. At that time the twig killing, or flagging, was found only on an area of about 500 acres near the city of Prescott. Investigations were begun in 1919 by W. H. Long, of the Bureau of Plant Industry, who thought the trouble might be caused by a species of *Cenangium*, presumably an indigenous and relatively harmless fungus. Long's unpublished records indicate that until 1933 the flagging showed considerable annual variation in intensity, but that the size of the affected area did not appear to be increasing beyond the original 500 acres.

Suddenly, in 1933 the twig killing reached epidemic proportions and was abundant over an area of about 30,000 acres in the Prescott National Forest, and two new heavily flagged areas were found in southwestern New Mexico. The Bureau of Plant Industry immediately started intensive work on the problem, primarily to determine whether some introduced organism might be involved, and in 1935 the Bureau of Entomology and Plant Quarantine began an investigation of the associated insects.[3] The research was continued until the spring of 1938, when it became clearly evident that a scale insect,

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[2] Although this paper is published under joint authorship, the pathological and entomological studies were carried out independently. The pathologists are responsible for the sections Histology of Affected Twigs and Associated Fungi and for certain insect data under the heading Pathological Analysis of Artificially Infested Twigs. Pathological research was directed by W. H. Long until his retirement on August 1, 1937, and later by L. S. Gill. The following at one time or another carried on investigative work on this problem for the Bureau of Plant Industry, Soils, and Agricultural Engineering, in cooperation with the Civilian Conservation Corps: Karl D. Butler, P. R. Frink, M. L. Lohman, H. C. Rhodes, V. O. Sandberg, F. R. Schroeder, Luther Shaw, C. B. Sumner, and W. H. Tharp.

[3] The entomological studies were carried out by the Bureau of Entomology and Plant Quarantine, under the general supervision of F. C. Craighead, in charge of the Division of Forest Insect Investigations, and Harold Morrison, of the Division of Insect Identification. In 1936 A. S. West, and later (April 1937) H. L. McKenzie, of the Division of Forest Insect Investigations, were assigned to Prescott for field work on the problem. During the two following seasons H. L. McKenzie conducted studies and experiments to determine the role the scale insect played in killing branches. Material assistance was contributed by the personnel of the Prescott National Forest, who made possible the setting up of the large-scale demonstration experiments.

Matsucoccus vexillorum Morrison,[4] was the primary cause of the trouble, that there was no immediate danger to the pine forests as a whole, and that local damage was of little economic importance.

OCCURRENCE OF MATSUCOCCUS AND FLAGGING INJURY

In 1934 a survey of the ponderosa pine forests of the United States was conducted by the Division of Forestry Pathology of the Bureau of Plant Industry, in cooperation with the Civilian Conservation Corps and the Forest Service. No new flagged areas were discovered in the course of that work but more intensive surveys, made subsequently, revealed that flagging existed at a number of widely scattered localities in Arizona and New Mexico. The known distribution of the *Matsucoccus* scale and flagging injury in 1942 is shown in figure 1. In 1943 several hundred acres of heavily flagged trees were discovered 10 to 15 miles west of Durango, Colo.

Flagging at Prescott increased rapidly from 1932 to 1934, then declined markedly from 1935 to 1937, but rose again slightly during 1938 and 1939. Flagging in 1938 was estimated to be about half as extensive as in 1934, and in 1939 it was about 37 percent of that in 1934. In 1940 it was extremely light. In 1946 it was moderate throughout the forest. Because of the removal and destruction of much affected material in the course of control work on the forest, these figures cannot be considered as representative of undisturbed natural conditions.

EFFECTS OF TWIG FLAGGING

Flagging usually occurs on trees less than 75 years old and is most conspicuous in dense stands of saplings or seedlings. Trees are rarely killed, although in years of heavy attack so many twigs are killed that at first glance many trees appear to be dead. Estimates of mortality among affected trees at Prescott during 1933 and 1934, years of severe flagging, ranged from 1 to 2 percent. A tally of 8,593 trees on 33 sample strips in the Prescott National Forest showed an average annual mortality of 0.13 percent for both 1938 and 1939. Most of the mortality was among trees less than 6 feet high, and no trees over 7 inches in diameter at 4½ feet above ground were killed.

A rather heavily flagged tree is shown in figure 2. Usually all the foliage on a flagged twig is killed, although sometimes green needles will remain behind the dead tip. The foliage of characteristically flagged twigs first turns light green, and the needles continue to fade, usually from their base outward, turning straw-yellow and finally light brown. Ordinarily the needles persist only for several months after the death of the twig, but sometimes they remain attached to it for more than a year.

Most of the injury appears in the spring, although in most infected areas a few flags may be seen early in the winter. The heavy period of twig killing at Prescott seems to coincide with warm, dry weather, which normally occurs between the middle of April and the middle of

[4] McKenzie, H. L. THE SEASONAL HISTORY OF *Matsucoccus vexillorum* MORRISON (HOMOPTERA: COCCOIDEA: MARGARODIDAE). Microentomology 8: 42–52, illus. 1943.

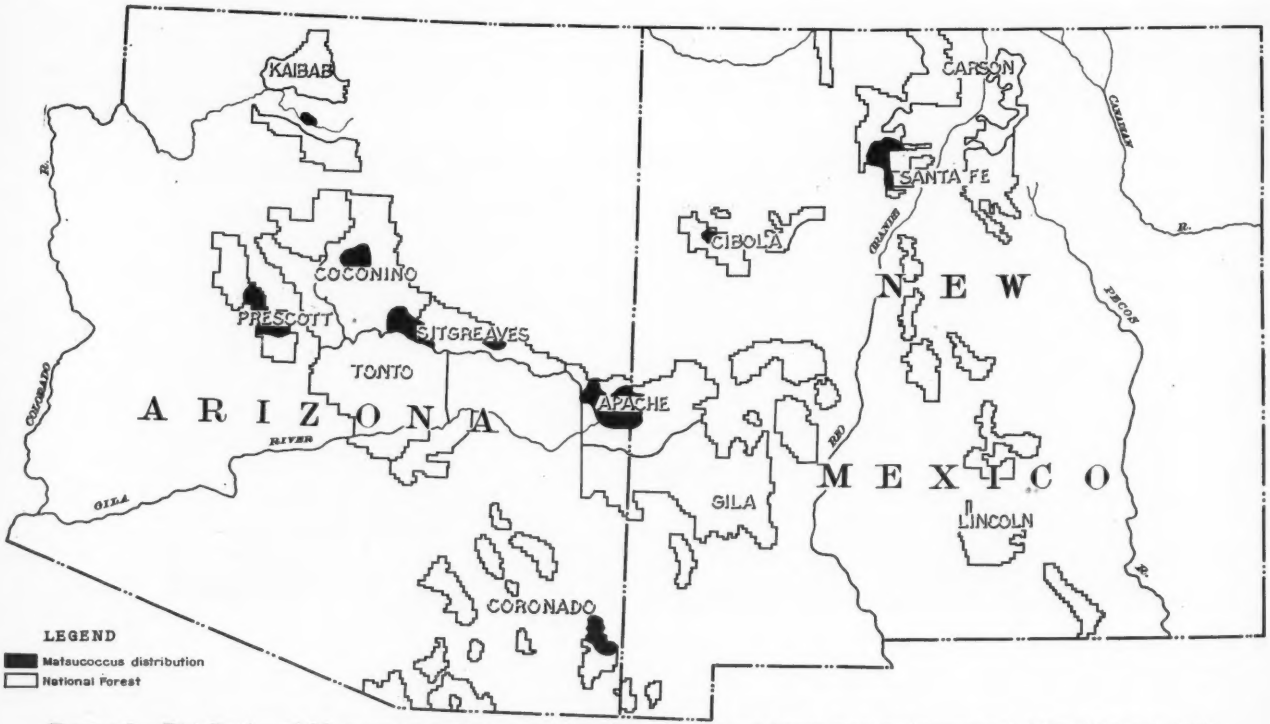

FIGURE 1.—Distribution of *Matsucoccus vexillorum* and flagging injury to ponderosa pine in Arizona and New Mexico in 1942. Affected areas are indicated in black.

May. Dry, warm winters are conducive to early flagging, which in some years has been conspicuous by the middle of January. As a rule, there is a marked drop in twig dying after the spring peak is

FIGURE 2.—Flagged ponderosa pine, Prescott National Forest. The dead twigs, or flags, are conspicuous by their light-colored, drooping foliage.

reached, and new killing after the middle of June is rare. Typical flagged twigs die, almost without exception, before the current year's needles emerge from the buds.

The old dead twigs from which the needles have fallen give a peculiar "staghorn" appearance to a tree, and trees that have been attacked for several successive years exhibit a singular crooked-branch habit and a thin crown (fig. 3). Flagging of the terminal shoot is not uncommon, and its frequent occurrence causes the tree to become badly malformed.

There seems to be no important relation between flagging and tree vigor or forest site. Vigorous, as well as suppressed, trees and twigs

FIGURE 3.—Ponderosa pine that has a "staghorn" appearance because it has been successively flagged for a number of years.

have been attacked on a wide variety of forest sites. It is possible that periods of severe twig killing are correlated to some extent with climatic conditions, but the relationship is not fully understood. The epidemic years of 1933 and 1934 at Prescott were below normal in precipitation and marked the last 2 years of a 4-year period of steadily declining tree growth.

HISTOLOGY OF AFFECTED TWIGS

Affected twigs invariably exhibit lesions, which are readily detected by the presence of necrotic bark. Lesions are most common on the

3- and 4-year-old growth, but may develop on any foliated part of the stem except the 1-year-old growth. The bark tissue turns brown and later becomes impregnated with resin. Extensive field observations indicate that, when bark necrosis is manifest during the fall in the form of small brownish areas in the living phloem, it may lead to flagging in the following winter or spring. The approximate center of these necrotic spots is usually a fascicle trace. The senior writer [5] has found that *Matsucoccus vexillorum* tends to settle at the base of the needle fascicles.

The necrotic spots enlarge and deepen in the phloem during the winter. When they reach the cambium and completely girdle it, the twig is killed. Fortunately pine trees seem to be well equipped to combat the progress of necrosis by walling off the diseased tissue with a thin layer of cork. Owing to this warding-off process, a great many lesions become arrested for every one that is able to cause a flag under natural conditions.

Late in the summer of 1937 tags were fastened to 77 twigs, each of which showed 1 or more bundles of dead or paling needles, believed to indicate a necrotic spot in the bark. By April of the following year none of the twigs had flagged. An examination of some of the twigs at that time showed that, of 169 fascicles containing paling needles marked on 34 twigs, 164 were associated with lesions only 1 of which did not appear to have been arrested. Of the twigs left undisturbed, none died later, a fact which suggests that all the lesions on them were arrested. The single active necrotic spot might have developed into a girdling lesion. The trees used in this experiment were in a heavily flagged locality, and several unmarked twigs on them flagged both before and after the experiment.

Where necrosis is arrested early in the development of a lesion, and does not reach the cambium, the effect is analogous to the formation of a bark plate. Normal phloem tissue continues to develop below the cork layer, and in time the affected tissue is sloughed off, leaving no trace of its former existence. This condition is illustrated in figure 4. Where necrosis reaches the cambium before being walled off by a cork layer, one of two things may happen—either cambial activity may be temporarily disrupted beneath the necrotic area, which is subsequently walled off, or an arc of the cambium may be killed, leaving a permanent record of the injury. Figure 5 illustrates these conditions.

All observations indicate that the progress of bark necrosis is limited to the season of its origin; that is, a lesion that originates in the fall either kills the twig by the following spring or is permanently arrested.

In addition to the bark necrosis, lesions are generally associated with necrotic fascicle traces. The latter turn brown, and the discoloration extends well into the wood, commonly as far as the central pith. When a small lesion circumscribes a single needle trace, this needle trace is almost invariably necrotic. In extensive lesions, notably lethal ones involving several years' growth, some of the fascicle traces are necrotic, whereas others show no indication of a pathological condition.

[5] See footnote 4, p. 34.

The xylem beneath necrotic bark generally becomes infiltrated with resin after necrosis is well advanced. Where partial lesions exist, the resined wood is wedge-shaped, a fact suggesting that it is

FIGURE 4.—Ponderosa pine twig with outer bark removed, showing extent of several small arrested lesions in living phloem.

bordered radially by medullary rays. In a girdling lesion a length of the entire wood cylinder may be impregnated with pitch. A lesion involving several inches of stem is usually accompanied by completely pitch-soaked wood for only a relatively short distance from its basal extremity.

FIGURE 5.—*A*, Cross section through a living twig, showing previous injury. The dark areas on the lower side are patches of necrotic bark which are being sloughed off. The dark streak at *a* is an arc of disturbed wood cells, indicating that a partial lesion occurred there at the beginning of the second year's growth. The following year a severe lesion killed the cambium from *b* to *c* and temporarily affected it for a greater distance. The killed area has been covered by 4 years of callus growth. *B*, Living twig showing callus formation over large arrested lesions, each of which killed an arc of the cambium.

The physiological processes leading to flagging have not been studied, but general observations indicate that it is probably the result of rapid necrosis. Many twigs in the process of flagging show necrotic bark for several inches, and often over several years' growth, while the needles are still green and succulent. Ponderosa pine twigs have been observed to remain alive for many months—some even for 2 years—after the removal of a band of bark about an inch wide. This suggests that something more than cambial girdling alone is necessary to cause flagging.[6]

EXPERIMENTS WITH MATSUCOCCUS

ARTIFICIAL INFESTATION OF TWIGS

The first tests to establish the nature of the relation of *Matsucoccus vexillorum* to flagging were begun in April 1936 (see footnote 3, p. 33). At that time 10 ponderosa pines were artificially infested with scales collected from heavily flagged trees in the forest. Egg masses of the scale, still attached to the branch nodes, were placed in small, thimble-shaped, copper-screen baskets, which were then fastened securely onto the twigs with fine copper wire (fig. 6). A total of 220 twigs were infested, and during the following season 46 percent of them flagged. In 1938, 5 additional twigs on these trees flagged, and the next year 4 more died.

In the spring of 1937 an experimental plot was established on the Wolf Creek area of Prescott National Forest. This plot (No. 1) included 15 trees, presumably free from natural scale attack and branch flagging, which were artificially infested at this time. On some of the trees the scale egg masses were placed on the branches by means of a camel's-hair brush, and on the remainder copper-screen baskets were employed. Seventy branches on 7 of these experimental trees were used as checks, empty copper baskets being attached in the manner used for introducing the scale insects.

Early in the spring of 1938, before there was much evidence of flagging, each infested twig was carefully examined in the field by the use of a 10× power hand lens to determine the population density of preadult scales. Population-density classifications were set up as heavy, medium, and light. The results of the work are included in table 1. The significant feature of these population studies is that, although 80 percent of the heavily infested branches flagged, those carrying only a light infestation or no scales, as well as the 70 check

[6] After examining this twig-blight area in April 1936, F. C. Craighead pointed out the similarity of this injury to "red twig" of balsam and other conifers, caused by mechanical injuries resulting in the destruction of the phloem. He said:

> It [the blighting of the twigs] is a most common phenomenon following logging operations where the pine sawyers (*Monochamus* spp.) breeding in the slash become abundant. These beetles gnaw off small areas of bark on living twigs. It is also common for several years after severe hail storms have caused bruised areas on the bark. The simplest physiological explanation seems to be based on the fact that most conifers secrete resin after a wounding of the phloem and cambium. This infiltration of resin often involves many annual layers of wood (turpentine faces) and stops all conduction through the area involved. In the case of the twigs a small sector to almost an entire cross section may become infiltrated with resin and conduction is greatly inhibited. From 1 to 5 years later, during periods of unusual stress, particularly following dry winter winds, when conduction is insufficient, the leaves turn brown.

Craighead believes that this type of injury can explain twig blight in the Prescott National Forest following the initial killing of the phloem by the scale. Other species of sucking insects apparently kill the twigs of conifers in much the same manner.

twigs, remained alive. Fourteen additional twigs on the trees in this plot flagged in 1939. It is probable that where no insects became established most of the eggs had hatched and the young larvae had already moved elsewhere before the egg masses were collected and placed on the twigs.

FIGURE 6.—Copper-screen baskets used to carry out the artificial infestation of ponderosa pine with *Matsucoccus vexillorum* scales.

TABLE 1.—*Results of the artificial infestation with Matsucoccus scale of 15 ponderosa pines in plot 1, Prescott National Forest, in 1937*

Population density, spring 1938	Twigs examined	Twigs flagged, summer 1938
	Number	*Percent*
None	88	0
Light	18	0
Medium	14	36
Heavy	30	80
Total	150	19

In the spring of 1938 two additional plots were laid out in the Prescott National Forest—plot 2 in the Wolf Creek area and plot 3 in the Copper Basin Divide. The Wolf Creek plot, at the time of establishment, was in a supposedly flag-free area, although Forest Service records indicated that some affected material had been removed in previous years. According to the Forest Service records,

the Copper Basin Divide plot had never shown any flagging. Most of the trees on this plot were vigorous "orchard" types. On plot 2, 90 trees and on plot 3, 60 trees were artificially infested with *Matsucoccus* scales. Table 2, which is based on data from all except 21 trees in plot 2, which were reserved for pathological studies by the Division of Forest Pathology, shows that from 36 to 54 percent of the artificially infested branches had flagged by the summer of 1939. Figure 7 shows the extent of flagging on one of the trees in plot 3.

FIGURE 7.—Tree No. 10, in plot 3, Copper Basin Divide, artificially infested with the *Matsucoccus vexillorum* scale in the spring of 1938. Eighty-two percent of the infested branches on this tree flagged in 1939.

TABLE 2.—*Results of the Artificial Infestation of Ponderosa Pine With the Matsucoccus Scale in Plots 2 and 3, Prescott National Forest in 1938*

Plot No.	Trees involved	Average height	Average diameter	Branches infested	Branches flagged, 1939
	Number	*Feet*	*Inches*	*Number*	*Percent*
2	69	12	2.8	702	36
3	60	16	3.8	628	54

In plot 4, established in 1938 in the Lynx Creek area, 80 naturally infested and flagged trees were marked, and 231 twigs carrying various numbers of adult females and egg masses were tagged for future observation. While the tendency for the twigs to flag was in direct proportion to the density of adult females and egg masses, the trend was less marked than in plots 2 and 3, where the preadult, or feeding stage, was used as an index of scale population. On plot 4, 72 percent of the twigs that carried heavy populations of adult females and egg masses flagged, whereas in both the medium and light infestations only 39 percent flagged.

During the 1938 reexamination of the flagging of artificially infested ponderosa pine trees on plot 1, it was discovered that there were heavy scale populations on flagged twigs and much lighter populations on the green infested twigs. A more thoroughly determination of scale-population density on flagged and green twigs was made, therefore, from infestations in the field near Prescott. Since preadult population counts have shown that the largest number of insects occur on the second year's growth, the 2-year-old part of the branch was used as a basis for comparison. A collection of 285 twigs was made at random from infested trees. The twigs were segregated by length of the second-year growth and were examined with the aid of a microscope. The results presented in table 3 indicate (1) that the population density of scale insects on flagged twigs is over twice that on green twigs [7] and (2) that flagging contributed to a high mortality of the *Matsucoccus* scale.

TABLE 3.—*Preadult Matsucoccus Scales Found on Second-Year Growth of Ponderosa Pine Collected at Random Near Prescott, Ariz., in 1938*

Flagged twigs						Green twigs					
Twigs involved	Second-year growth		Scales			Twigs involved	Second-year growth		Scales		
	Average length	Average diameter	Living	Dead	Average per twig		Average length	Average diameter	Living	Dead	Average per twig
Number	*Inches*	*Inches*	*Number*	*Number*	*Number*	*Number*	*Inches*	*Inches*	*Number*	*Number*	*Number*
20	0.9	0.4	21	366	19.3	28	1.2	0.3	211	67	9.9
20	2.1	.3	41	559	30.0	28	2.0	.2	345	83	15.3
42	3.0	.3	101	1,309	33.6	31	3.0	.3	359	109	15.1
22	4.0	.3	67	732	36.3	12	4.0	.3	185	55	20.0
12	5.0	.5	51	585	53.0	19	5.0	.5	280	75	18.7
15	6.0	.5	43	856	59.9	13	6.0	.5	220	40	20.0
4	7.0	.5	4	368	93.0	4	7.0	.6	57	27	21.0
4	8.0	.5	18	302	80.0	1	8.0	.5	22	4	26.0
1	9.0	.3	1	40	41.0	2	9.0	.4	40	21	30.5
3	10.0	.8	20	185	68.3	4	10.0	.7	98	30	32.0
143	----	----	367	5,302	39.6	142	----	---	1,817	511	16.4

[7] The scale populations on flagged twigs are undoubtedly higher than the figures show, since a large number of needles, and consequently of insects, were lost in handling. For example, a study of 57 flagged and 62 green twigs (second year's growth) showed that only 27 percent of the needles on the flagged twigs remained, as compared with 80 percent on the green twigs.

Even though it had been demonstrated by actual counts that a large population of the *Matsucoccus* scale was always present on flagged branches, there was still the question whether killing lesions developed only on the parts of the stem where scales were present. Therefore, it was deemed advisable to restrict the scales to a specific year's growth by applying barriers of a commercial tree tanglefoot before introducing the scales. Two types of barrier were used, one consisting of a thin layer of the tanglefoot smeared directly on the stem, and the other of an absorbent-cotton band wrapped around the stem, over which was placed a strip of ½-inch crepe-paper masking tape (fig. 8, *A*). Tanglefoot was then applied to the tape to prevent it from coming in contact with the bark surface and possibly causing injury to the twig.

The barriers were placed at the extremities of a year's growth and were generally effective in restricting the scales, although in a few instances some of the insects escaped (fig. 8, *B*). Scales were introduced between the barriers by placing egg masses in small, thimble-shaped, copper-screen baskets, which were securely held to the stem with fine copper wire.

Thirty-six trees, 17 on plot 2 and 19 on plot 3, were artificially infested in this manner. Of these trees 22 had barriers on the second year's growth (fig. 9) and 14 had them on the third year's growth. The results of the infestations are given in table 4, which shows that 34 and 35 percent of the twigs with scale restrictions on the second-year growth flagged, whereas flagging occurred in only 14 and 23 percent of the third-year-growth restrictions. In nature, as has already been stated, girdling lesions tend to be much less numerous on the second year's growth than on that of the third and fourth years. The girdling lesions occurred only within that part of a branch where scales were restricted, and in no case did killing extend beyond the proximal barrier toward the main stem (fig. 8, *B*). General observations on many infested twigs where few or no scales became established and which showed no flagging, indicated that neither the barriers nor the copper baskets were alone responsible for the development of girdling lesions.

TABLE 4.—*Artificial infestation of 2- and 3-year-old growth of ponderosa pine twigs with Matsucoccus scales, in plots 2 and 3, Prescott National Forest in 1938*

Plot No.	Part of branch used (age of wood)	Trees			Twigs	
		Involved	Average height	Average diameter breast high	Infested [1]	Flagged [2]
	Years	*Number*	*Feet*	*Inches*	*Number*	*Percent*
2	2	10	12.5	2.6	206	35
	3	7	16.1	5.1	109	14
3	2	12	11.7	3.1	522	34
	3	7	10.5	3.9	238	23

[1] The artificial-infestation experiments in restricting the scale to certain year's growth of the stem were conducted from April 28 to May 13, on plot 2, and from May 9, to 12, on plot 3.
[2] Flag readings were taken on July 24–26, 1939, on plot 2, and on June 26, 1939, on plot 3.

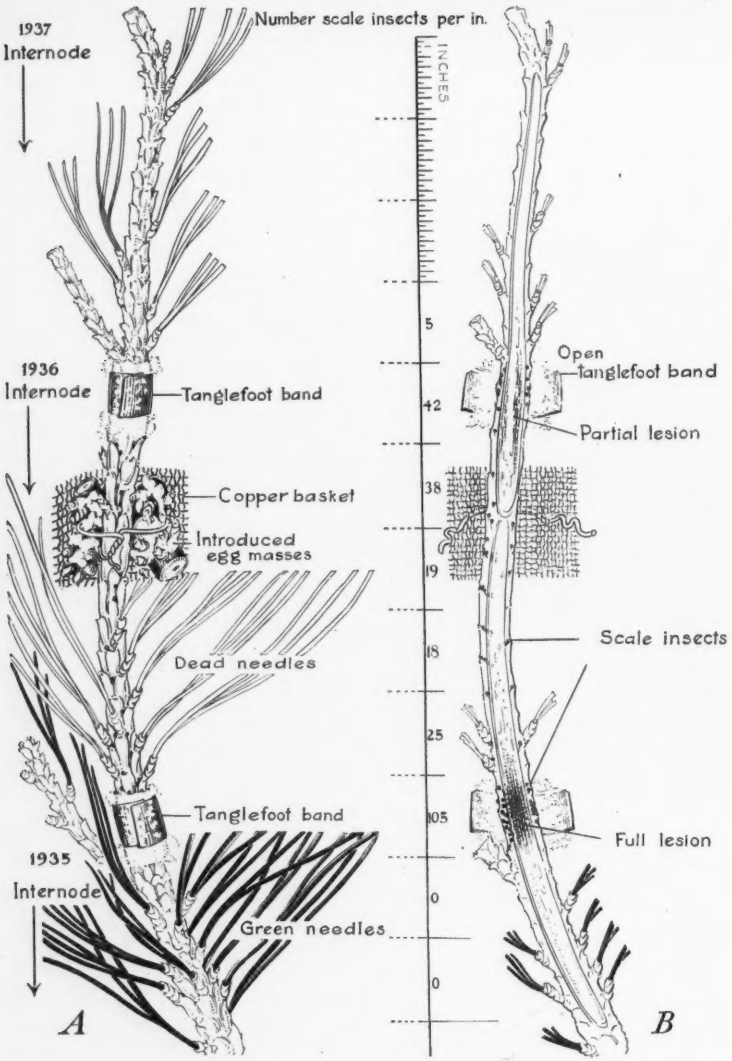

FIGURE 8.—Cotton-tape bands used to restrict *Matsucoccus vexillorum* scales to certain year's growth on the pine branches. *A*, The scale insects were introduced between the barriers by placing egg masses in copper-screen baskets, which were held securely to the stem with fine copper wire. *B*, The scale insects successfully established on test twigs were counted approximately a year after initial artificial introduction. The twigs were sliced with a pocketknife to ascertain killing lesions. There appeared to be a definite correlation between scale population and such lesions.

During the summer of 1939, 60 of the 1,075 branches originally infested with scales were cut and examined in the laboratory. The copper baskets and barriers were removed, and the needles were cut off rather short to permit observation of the insects with the low-power binocular microscope. The branch sections were diagramed

FIGURE 9.—Experimental tree No. 37, on plot 3 in Copper Basin Divide, near Prescott, Ariz., which had barriers applied to the second year's (1937) growth only. Fifty-two percent of the infested twigs flagged from lesions in the second year's growth.

to actual size on drawing paper and measured off into 1-inch intervals. The number of preadults found on each inch of stem was recorded in the corresponding interval on the diagram. After the counts were completed, the stems were carefully sliced with a pocketknife, to determine the exact position of the lesions (fig. 8, *B*).

When used alone, the tape barriers were more effective than the tanglefoot. The scale larvae apparently preferred to settle under the cotton bands, because these afforded them some protection. As many as 225 preadults have been observed under one band. The results of the scale counts on the 60 twigs with barriers indicate that, when there is

an average population density of 100 or more preadult scales of the same generation per linear inch of stem with a diameter of ½ to ¾ inch, killing lesions will be associated with these insects.

PATHOLOGICAL ANALYSIS OF ARTIFICIALLY INFESTED TWIGS

The 21 artificially infested trees on plot 2 that were reserved for pathological studies by the Bureau of Plant Industry had a total of 483 artificially infested twigs. On 294 of them the insects were not restricted, on 119 they were restricted to the 3-year-old (1936) growth, and on 70 they were restricted to the 2-year-old (1937) growth, both types of barriers previously described having been used. These three classes of restrictions will hereafter be referred to as series A, B, and C. Five approximately equal random collections from these trees were made as follows: (1) In December 1938, (2) in January 1939, (3) in March 1939, (4) in April 1939, and (5) in May 1939.

Scale Population

The twigs were examined to ascertain whether the scales had become established. This was determined by the presence or absence of preadults on twigs of collections 1 to 4, and by presence or absence of egg masses or preadult "cases" on twigs of collection 5, since the preadults had developed into adult females by May. In collections 1 to 4 an estimate of scale intensity on each year's growth was obtained on the basis of preadult population. The fifth collection was considered unreliable for this purpose. A record was also kept of instances in which it could be determined with certainty that the preadults located within the bounds of a lesion were dead.

Lesions

A record was kept of the number and size of lesions found on each year's growth. Lesions ranged in size from small but readily visible necrotic spots in the bark at the base of needles to diffuse necrosis extending over two or more years' growth. In large lesions, covering several years' growth, the probable age of the stem portion on which they originated, as determined by resin infiltration and general necrotic appearance, was recorded.

Fungi

Cultures were made from all lesioned twigs in collections 1 to 4. The twigs were surface-sterilized with 1:1,000 mercuric chloride, the outer bark was removed, and small chips of necrotic tissue were planted on malt-agar plates. The number and type of fungus colonies developing from the chips were then recorded.

For all five collections, records were also kept of all lesioned twigs bearing fruiting bodies of *Cenangium* sp., either visible on the surface or beneath the bark. During the period of the first four collections (December to April) there appeared to be no significant increase in the average size or number of lesions, nearly all of which occurred on the 3- and 4-year-old growth. The fifth collection (May) showed in addition an abundance of small lesions on the 2-year-old growth. No explanation can be offered at this time for the sudden and late appearance of lesions on the 1937 growth.

General Results

The general results obtained in series A, B, and C are shown in table 5. No lesions were found on twigs on which scales had not become established.

Table 5.—*Pathological Analyses of 21 Artificially Infested Trees From Collections 1 to 5, Plot 2, Made December 1938 to May 1939, at Prescott, Ariz.*

Examinations	Series A	Series B	Series C
	Number	*Number*	*Number*
Twigs artificially infested	294	119	70
Twigs upon which scales became established	211	94	43
Lesioned twigs with scales	109	67	16
Lesioned twigs that flagged	29	1	1
Lesioned twigs that probably would flag	32	16	1
Twigs with small lesions only	48	50	14

The percentage of lesioned twigs that flagged in the artificial-infestation studies was markedly higher than seems to be the case in nature. Presumably this was due to the fact that the artificially infested twigs, in general, carried greater scale populations than would infested twigs in a sample taken at random in nature. Most of the experimentally infested twigs with only small lesions would probably have lived.

In collections 1 to 4 (December to April) fruiting bodies of *Cenangium* were present on 36 percent of the lesioned twigs. In 78 percent of the lesioned twigs there were dead scales over lesioned tissue.

These analyses indicate that scales are probably the primary cause of lesion formation, since lesions occurred only on twigs where scales were present. It is also evident that some infested twigs do not develop lesions. In series A 52 percent and in series B 71 percent of the twigs on which scales were present developed lesions. The data for series C are not considered comparable, because practically no lesions were found until May.

Table 6.—*Fungi Cultured From 21 Artificially Infested Trees, Collections 1 to 4, Plot 2, December 1938 to April 1939, at Prescott, Ariz.*

Series	Twigs cultured			Twigs producing—		
	Total	Producing fungi	Sterile	*Cenangium* sp.	Saprophytes [1]	Other fungi
	Number	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
A	68	85	15	71	34	7
B	26	85	15	62	42	8
C	2	100	0	[2] 50	50	0
Total	96	85	15	68	36	7

[1] Black, fast-growing, ubiquitous saprophyte.
[2] Lesion occurred on 1935 growth.

Table 6 gives data on the fungi cultured from samples taken from collections 1 to 4. *Cenangium* sp. is the fungus most frequently associated with blight lesions at all stages of their development.

Analysis of the artificially infested twigs in series A showed that lesions originated only where scales were present. On 164 twigs 4 or

more years of age on which scales became established, infestations were found on 152 2-year-old segments, 138 3-year-old segments, and 71 4-year-old segments. No lesions originated in infested growth of 1937 (2 years old) until the May collection, 33 originated in infested growth of 1936, and 38 in infested growth of 1935. This suggests that, although the heaviest population of scales is usually on the 2-year-old growth, it is possible that the mere presence or absence of scales on the 3- or 4-year-old growth may be a more important factor in the formation of lesions than is scale-population density here or elsewhere on the twig.

ASSOCIATED FUNGI

The fungus most frequently associated with the so-called "twig blight" is a species of *Cenangium* that is morphologically and physiologically similar to *C. ferruginosum* Fr. (*C. abietis* Pers. ex Rehm.). Duby. Long [8] considered this fungus to be an important and beneficial agent in the self-pruning of ponderosa pine. *Cenangium* sp. is often isolated from lesions, and it invariably fruits abundantly on flagged twigs. It is not uncommon to find the black stromata of this fungus beneath the bark of lesioned twigs that probably would have flagged although the needles were still green and fairly succulent. This suggests that the fungus becomes established well in advance of the death of the twig. Between November 1934 and March 1938 it was isolated from 31 percent of 430 incipient nongirdling lesions cultured, and from 54 percent of 458 flags. In the different lots studied during this period these percentages ranged from 8 to 57 percent of the lesions and from 35 to 98 percent of the flags.

Schwartz [9] attributed a twig-dying of pine in Europe to *Cenangium abietis*, but did not verify his contention with inoculation experiments. More recently Liese [10] stated that the European disease, which is similar in some respects to the twig flagging herein described, results from the combined effects of a gall midge (*Cecidomyia brachyptera*) and a parasitic fungus. By association, *Cenangium abietis* appeared to be the most likely fungus, although neither its connection with the midge nor its parasitic nature had been positively established.

A small and inadequate amount of isolation work from various stages of *Matsucoccus vexillorum* from Arizona has failed to indicate that it is a vector of a micro-organism.

In addition to *Cenangium* sp., 10 other fungi and several bacteria have been isolated from lesioned twigs. None of these has been found as frequently as *Cenangium*, nor have inoculations demonstrated that they are involved in the twig killing. Of the fungi, one tentatively identified from its imperfect stage as *Scoleconectria* sp. exhibited parasitic tendencies to a somewhat greater extent than the others. It was rather infrequently isolated from recently lesioned

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[8] LONG, W. H. THE SELF PRUNING OF WESTERN YELLOW PINE. Phytopathology 14: 336–337. 1924.

[9] SCHWARTZ, F. DIE ERKRANKUNG DER KIEFERN DURCH CENANGIUM ABIETIS. 126 pp., illus. Jena, 1895.

[10] LIESE, J. ZUM TRIEBSTERBEN DER KIEFER. Deut. Forstwirt. 17: 381–383. 1935.

tissue, and hundreds of inoculations with it failed to produce flags, except where the technique was so drastic that most of the checks were killed.

SUMMARY AND CONCLUSIONS

Research on the so-called "twig blight" of ponderosa pine in the Southwest indicates that the flags and lesions characteristic of the trouble occur only on twigs that have been attacked by the scale insect *Matsucoccus vexillorum* Morrison. This scale is therefore believed to be the primary cause of the blight. Although heavy flagging appears only in areas where the insect is abundant, infested twigs frequently develop no lesions.

The intensity of flagging in areas infested with *Matsucoccus* varies widely from year to year. The epidemic conditions which existed in 1933 and 1934 have been followed by 12 years of relatively low, though somewhat fluctuating, intensity. Since scale mortality was much higher on "flags" than on green infested twigs, it is logical to assume that during epidemic years the scale population of the area becomes drastically reduced, and several seasons may be necessary for it to build up to the point where damage to the pine again becomes conspicuous.

Damage to the forest by the blight was found to be lighter than was at first feared. Tree mortality has been insignificant and has occurred primarily among seedlings and saplings. Since the forest types affected by the trouble are well stocked and are valued primarily for watershed protection or recreational use rather than timber production the damage is of no great economic importance. There is no indication that this twig blight will in any way endanger the pine forests of the United States.

Eleven fungi and several bacteria occur rather frequently in flagged twigs or in lesioned tissue of living twigs. A fungus morphologically similar to *Cenangium ferruginosum* is the one most commonly associated with lesioned tissue, and it almost invariably fruits on flagged twigs. Inoculations with these fungi and bacteria indicate that none of them are sufficiently parasitic to cause flagging independently. The lesions seem to originate in the phloem at fascicle traces, a condition that suggests close association with the scale, since the preadults usually settle in the axils of the needle fascicles. Many lesions are arrested by the action of a pathological cork cambium which walls off the necrotic tissue before a lethal girdle can be effected.

INHERITANCE OF WEIGHT PER UNIT LENGTH OF CULM AND OTHER CHARACTERS IN KANRED × COPPEI WHEAT[1]

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INTRODUCTION

Lodging of the cereal crops has long been a subject of study. On land high in fertility or in seasons of abundant precipitation, it may often become a serious factor in the harvesting of the crop and may cause heavy financial loss to the grower. With the advent of the small combine-harvester-thresher in the more humid areas where cereals are grown, the problem becomes increasingly important.

Mechanical devices of various types have been invented to test lodging resistance of small grains in the laboratory and thus aid in selecting strains resistant to lodging. Some of these devices have been found satisfactory, while others have been reported as unsatisfactory. At Texas Substation No. 6, Denton, Tex., weight per unit length of culm near the base of the plant (herein referred to simply as weight per unit length) has been successfully used for a number of years to test the relative resistance to lodging of varieties and strains of winter wheat. Extensive studies of varieties under field conditions show that this measure is significantly correlated with lodging in the field. The method has been found less satisfactory for oats and barley.

The present study is concerned with measurements of weight per unit length, of breaking strength of the culm near the base of the plant (herein referred to simply as breaking strength), and of other morphological characters in plants of the early segregating generations of a hybrid between Kanred, a lodging-susceptible common hard red winter wheat (*Triticum aestivum* L. (*T. vulgare* Vill.)) having low weight per unit length, and Coppei, a lodging-resistant club wheat (*T. compactum* Host) having high weight per unit length. The purpose was to study the variability and inheritance of these characters and to determine to what extent measurements of them in early generations might serve as an aid in isolating lines that maintain high weight

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[2] The writer expresses his appreciation to H. K. Hayes, chief, Division of Agronomy and Plant Genetics, University of Minnesota, and to K. S. Quisenberry and S. C. Salmon, Division of Cereal Crops and Diseases, for helpful suggestions throughout the course of this experiment and in the preparation of the manuscript.

per unit length or other desired characteristics in later generations. The plan was to determine the correlation between morphological characters and lodging under natural conditions in the field; but, as no lodging occurred during the period of study, this phase of the experiment could not be carried out. As the parent varieties Kanred and Coppei differed in respect to presence of awns, pubescence of glumes, and spike length, the inheritance of these characters was studied in the same material.

REVIEW OF LITERATURE

The literature on lodging of small grains is extensive. Rather complete reviews were made by Welton and Morris (*14*),[3] the Imperial Bureau of Plant Genetics, School of Agriculture,[4] and Phillips, Davidson, and Weihe (*8*). The papers reviewed pertained largely to causes of lodging, relation of morphological characters to lodging, and mechanical tests for measuring resistance to lodging. No reports on the inheritance of lodging resistance in wheat as determined mechanically were found. Such methods were used, however, by Smith (*11*) on oats, by Bose, Aziz, and Bhatnagar (*3*) on barley, and by Ramiah and Dharmalingam (*9*) on rice. Heritable differences in lodging resistance have been recognized by many workers.

Basing their distinctions upon visual observations and evaluations of hybrid progenies of wheat crosses, several workers have shown that strength of straw is an inherited character. Clark, Florell, and Hooker (*4*) found an association between awnedness and tendency to lodge. Goulden and Neatby (*5*) found a genetic linkage between weak straw and mature-plant resistance to stem rust. Kilduff (*7*) studied the tendency to lodge in two crosses on Kota wheat. He found in one a significant correlation between bunt resistance and weak straw and in the other a correlation between bunt resistance and strong straw. Waldron (*13*) also studied lodging resistance in a cross involving the variety Kota. He found that the progeny ranged from strains having weaker straw than Kota to strains about midway between the parents in lodging resistance. Torrie (*12*) classified the F_3 population of two crosses on the variety Caesium on the basis of a lodging index computed from the percentage lodged and the angle of lodging. No genetic interpretation was proposed, but the F_3 lines ranged from the weak-strawed parent to the strong-strawed.

The most extensive use of a mechanical testing device on hybrid populations was made by Smith (*11*), who tested several hundred F_2 plants from an oat cross and compared their reactions with those of their F_3 progenies. He concluded that measurements of the F_2 plants alone are not adequate to determine resistance to lodging. Hamilton (*6*), working in Canada, also found that the weight per unit length is insufficient in itself to test lodging resistance of oat varieties.

MATERIAL AND METHODS

The present study of the inheritance of morphological characters that may be associated with lodging was started in 1932, when the

[3] Italic numbers in parentheses refer to Literature Cited, p. 71.

[4] IMPERIAL BUREAU OF PLANT GENETICS. LODGING IN CEREALS. 8 pp. Cambridge. 1931. [Processed.]

first cross was made. Breaking-strength tests were made on varieties of wheat grown in field plots before that time, and the data were used as a guide in selecting parental material.

For the lodging-susceptible parent, the common hard red winter wheat variety Kanred was selected. Kanred, a pure-line selection from the Crimean (Turkey) variety, is of moderate height and has an awned, slender spike with white, glabrous glumes. It tillers abundantly and, except for susceptibility to leaf rust, is well adapted to conditions in north-central Texas.

The lodging-resistant parent selected was Coppei, a club wheat having awnless, compact spikes, pubescent glumes, short culms, and relatively low tillering ability in Texas. It is poorly adapted to Texas because of its high susceptibility to leaf and stem rusts. In the present study, however, these diseases were controlled by dusting with sulfur. In varietal comparisons of weight per unit length in another experiment, the 5-year average weight per unit length of Coppei was 14.3 gm. per five-culm sections compared with an average of 8.4 gm. per five-culm sections for Kanred.

All tests were made on single plants grown in 10-foot nursery rows spaced 12 inches apart. Plants were spaced accurately 3 inches apart in the rows by dropping the seed through holes in a board. After the plants emerged, missing hills were replanted with a variety that could be recognized and discarded at maturity. At harvesttime plants surrounded by perfect stands were pulled and placed under cover for future testing.

The characters studied in all or some of the seasons included breaking strength, weight per unit length, total weight of culm, plant height, diameter of culm near the base of the plant, length of lower internode, weight of head, length of head, head type, awn type, and pubescence of glume. Tests and measurements of these characters were made as follows: Culms were cut off at the ground level; the tallest culm was measured for plant height, length of internode, and head length; and data were then recorded on head type, awn type, and presence of pubescence of glumes. Heads were then removed from all culms and five selected at random were weighed; culms were then weighed in units of five for the weight of culm.

In 1934, 1936, and 1937 the tests of breaking strength were made by means of the Salmon (*10*) breaking-strength-of-straw machine; again the unit sample was five culms. When possible, two or more tests per plant were made and the results were averaged.

Weight per unit length was obtained by cutting sections of culm 10 cm. long from the region of the first straight internode. Such a section included one node and parts of two internodes. Sections were cut from five culms at one time by means of the cutter shown in figure 1. These sections were weighed on a scale sensitive to 0.01 gm. Two or more tests were made on each plant having sufficient tillers.

After the culm sections were weighed, diameter of culm was determined by placing the five sections side by side and measuring the overall diameter with a vernier caliper.

Because of the large seasonal influence on morphological characters, it was considered desirable to grow as many generations as possible each season. The cross was remade each year in order to have several generations available for study. The 1934 plantings consisted of the

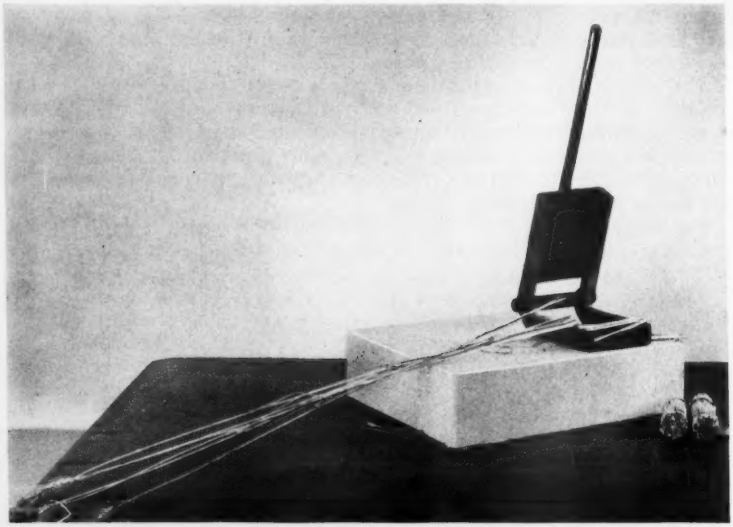

FIGURE 1.—Straw cutter used to cut 10-cm. sections of culms for determination of weight per unit length.

parents and the F_1 and F_2 populations of the hybrid. All plantings were winterkilled in 1935. The 1936 material consisted of parents, F_1 and F_2 populations, and F_3 progeny rows. Twenty plants selected at random were tested from each of the progeny rows. Parents and F_4 progeny rows were grown and tested in 1937. The F_3 plants selected for planting the F_4 progeny rows included extremes as well as random selections.

Because of inadequate parental material for comparison with hybrids in the early tests and unfavorable seasonal conditions, the test was redesigned on a more extensive scale in 1940. Seasonal conditions were favorable, and normal plants were produced. Four hundred and eighty plants from the F_2 populations, 31 F_1 plants, and 200 plants from each of the parent populations were selected at random for testing. In 1941 the tests consisted of duplicate progeny rows of 100 F_3 lines. Ten progeny lines from each parent were grown for comparison. Twenty randomly selected plants were tested from each duplicate row. Excessive precipitation throughout the 1941 season was unfavorable for the development of the plants.

The 1942 plantings were destroyed by green bugs. In 1943, 128 F_4 lines were grown in duplicate progeny rows along with 25 lines from each parent for comparison. Twenty plants selected at random were tested from each row. Seed for planting the F_4 was from plants within F_3 lines representing the extremes in weight per unit length and in variability. Low temperatures during the winter of 1943–44 damaged the planting, killing all progeny rows of the Coppei parent and many hybrid progeny rows. Only 83 lines could be tested, and both replications were available for only 39 lines.

EXPERIMENTAL RESULTS

VARIABILITY OF MORPHOLOGICAL CHARACTERS

Because of the importance of environmental factors it was desirable to determine their influence on the characters being studied. This can be approximated by comparing the coefficients of variability of the parental and F_1 plants, in which all the variability should be environmental as no genetic segregation is expected, with those of the F_2 population grown under the same conditions, in which both genetic segregation and environment play a part. No special planting was made for this comparison; but, as the selections planted for the study of inheritance of weight per unit length were made without regard for other characters, the population may be considered random. Such data for the 1934, 1936, and 1940 seasons are given in table 1.

TABLE 1.—*Variability of certain plant characters of parents and F_1 and F_2 populations of the wheat cross Kanred × Coppei, Denton, Tex., 1934, 1936, and 1940*

Type of material and parent or cross	Year	Coefficient of variability for—							
		Breaking strength	Weight per unit length	Weight of 5 culms	Diameter of 5 culms	Plant height	Length of lower internode	Weight of 5 heads	Head length
Homogeneous:		*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Kanred parent	1934	16.19	13.02	14.33	5.96	5.47	14.37	18.07	10.53
Do	1936	8.68	7.43	11.21	5.78	4.77	16.75	4.58	9.63
Do	1940	------	12.91	18.24	8.11	4.78	10.34	18.55	15.37
Coppei parent	1934	10.61	9.00	19.55	6.95	7.44	12.68	20.68	9.44
Do	1936	1.35	7.72	12.38	5.81	5.63	8.63	13.73	5.66
Do	1940	------	9.86	14.11	7.27	4.88	16.79	15.11	10.61
Kanred × Coppei F_1	1934	13.31	11.47	11.77	5.39	4.44	11.83	15.77	9.49
Do	1936	.34	6.62	16.19	4.18	4.27	15.41	16.48	6.37
Do	1940	------	9.10	9.96	4.37	3.88	18.22	13.19	9.83
Mean	------	8.41	9.68	14.19	5.98	5.06	13.89	15.13	9.66
Heterogeneous:									
Kanred × Coppei F_2	1934	14.82	19.18	20.18	8.67	8.74	16.42	26.65	25.58
Do	1936	11.63	12.60	11.65	5.07	7.42	16.89	15.10	36.90
Do	1940	------	16.16	18.47	8.69	8.46	20.02	21.14	34.52
Mean	------	13.23	15.98	16.77	7.48	8.21	17.78	20.96	32.33

The variability of characters, as measured by the coefficient of variability, is of approximately the same order in both homogeneous and heterogeneous material (table 1). The least variable character in most classes was plant height followed closely by diameter of culm. In the homogeneous material weight of head was the most variable character, followed closely by weight of culm and length of lower internode. All characters were more variable in the F_2 as would be expected. Because of the wide difference in head types of the parents, head length and weight of heads were highly variable in the F_2 populations. The data indicate that one-half to three-fourths of the total variability of the heterogeneous material may be due to environmental influences.

VARIABILITY AND INHERITANCE OF WEIGHT PER UNIT LENGTH

In order to determine whether the parental varieties were pure for the characters under investigation and what variability was to be

expected in uniformly spaced plant material, random selections and others representing the extremes in weight per unit length of each parent were grown and tested under the same conditions as the hybrid populations each season. The data for parents and early hybrid generations for 1934, 1936, and 1940 are given in table 2. As none of these tests could be replicated, the data are presented in convenient, arbitrary intervals in the table.

It is evident from the data that the parents are statistically different in mean weight per unit length, although the ranges overlapped in 1940. The variability of the parents was high in some seasons; but this appears to be environmental, since the progeny lines grown from plants having widely different values were rather uniform the following season. It appears, therefore, that the parents were essentially homozygous for the characters studied. The F_1 plants, while intermediate between the parents each season, tended to approach the Coppei parent in mean weight per unit length. The range of weight per unit length for the F_2 was much greater than for the F_1 or parental material, as would be expected.

The results of tests of the F_3 progeny lines in comparison with parent progeny lines in 1936 and 1941 are given in table 3. The lines are grouped by weight per unit length and coefficient of variability of weight per unit length with class centers based on the standard error of a difference between two lines. The data show that a majority of the F_3 lines were intermediate between the parents but that the range of F_3 lines recovered was from the lowest Kanred lines to well within the range of the Coppei parent. The recovery of F_3 lines having a wide range of weight per unit length indicates that inheritance of this character involves multiple factors. In both seasons F_3 lines approaching homozygosity, as indicated by low coefficient-of-variability values, were recovered in a wide range of weight-per-unit-length classes.

The analysis of variance of the F_3 progeny lines grown in two replications in randomized blocks in 1941 is given in table 4. The least significant difference between two strains at the 5-percent level was 0.105 gm. The differences between progeny lines are highly significant.

Correlation coefficients were calculated between the weight per unit length of F_2 plants of 1934 and the mean of their F_3 progeny lines grown in 1936 and between the F_2 plants of 1940 and the mean of their F_3 progeny lines grown in duplicate rows in 1941. These coefficients were 0.414 and 0.609, respectively. Both values exceed the 1-percent level and show that F_2 plants may be expected to transmit the characteristics of their weight per unit length to a fair proportion of their progeny lines. The relation of the two generations in the more accurate test of duplicate progeny rows in 1941 is shown in a scatter diagram (fig. 2).

Tests of selected F_4 progenies were made in 1937 and 1943, the latter in duplicate plantings. Data for these are given in table 5. As in table 3, the data are grouped by weight per unit length and coefficient of variability of weight per unit length with class centers based on the standard error of a difference between two classes in the 1943 test. The 1937 data are included in the same classes for con-

TABLE 2.—*Frequency distribution for weight per unit length of plants of parents and F_1 and F_2 populations of the wheat cross Kanred × Coppei, Denton, Tex., 1934, 1936, and 1940*

Year and parent or cross	Plants with indicated weight per unit length (grams) per 5-culm sections												Total plants	Mean	Standard deviation	Coefficient of variability
	0.31–0.40	0.41–0.50	0.51–0.60	0.61–0.70	0.71–0.80	0.81–0.90	0.91–1.00	1.01–1.10	1.11–1.20	1.21–1.30	1.31–1.40	1.41–1.50				
1934	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Grams*	*Gram*	*Percent*
Kanred parent	13	7	0	0	0	0	0	0	0	0	0	0	20	0.430	0.056	13.02
Coppei parent	0	0	0	6	6	8	0	0	0	0	0	0	20	.778	.070	9.00
Kanred × Coppei F_1	0	0	13	6	7	0	0	0	0	0	0	0	26	.654	.075	11.47
Kanred × Coppei F_2	4	30	47	46	30	13	3	0	0	0	0	0	173	.656	.126	19.18
1936																
Kanred parent	0	0	0	5	13	7	0	0	0	0	0	0	25	.754	.056	7.43
Coppei parent	0	0	0	0	0	0	1	8	6	6	0	0	21	1.138	.088	7.72
Kanred × Coppei F_1	0	0	0	0	0	0	2	1	2	0	0	0	5	1.056	.070	6.62
Kanred × Coppei F_2	0	0	1	8	37	51	54	33	1	0	0	0	185	.897	.113	12.60
1940																
Kanred parent	0	0	3	25	72	71	22	7	0	0	0	0	200	.805	.104	12.91
Coppei parent	0	0	0	0	0	5	25	55	64	39	10	2	200	1.126	.111	9.86
Kanred × Coppei F_1	0	0	0	0	0	1	5	10	11	4	0	0	31	1.088	.099	9.10
Kanred × Coppei F_2	0	3	19	60	124	144	84	31	15	0	0	0	480	.829	.134	16.16

TABLE 3.—*Frequency distribution for weight per unit length grouped by coefficient-of-variability classes for parental and F_3 progeny lines of the wheat cross Kanred × Coppei, Denton, Tex., 1936 and 1941*

Year and parent or cross	Coefficient-of-variability class	Lines with indicated weight per unit length (grams) per 5-culm sections											Total lines
		0.567–0.619	0.620–0.672	0.673–0.725	0.726–0.778	0.779–0.831	0.832–0.884	0.885–0.937	0.938–0.990	0.991–1.043	1.044–1.096	1.097–1.149	
1936	*Percent*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Kanred parent	5.1–8.5	0	0	0	1	0	0	0	0	0	0	0	1
Coppei parent	5.1–8.5	0	0	0	0	0	0	0	0	0	0	1	1
Kanred × Coppei F_3	5.1–8.5	0	0	0	0	2	1	3	0	0	0	0	6
	8.6–12.0	0	0	6	13	27	15	9	5	2	0	0	77
	12.1–15.5	0	0	3	11	19	17	6	3	0	0	0	59
	15.6–19.0	0	0	0	2	3	1	2	0	0	0	0	8
	19.1–22.5	0	0	0	2	0	0	0	0	0	0	0	2
	22.6–26.0	0	0	0	0	0	0	1	0	0	0	0	1
Total		0	0	9	28	51	34	21	8	2	0	0	153
1941													
Kanred parent	5.1–8.5	0	3	0	0	0	0	0	0	0	0	0	3
	8.6–12.0	4	1	0	0	0	0	0	0	0	0	0	5
	12.1–15.5	2	0	0	0	0	0	0	0	0	0	0	2
Total		6	4	0	0	0	0	0	0	0	0	0	10
Coppei parent	5.1–8.5	0	0	0	0	0	0	0	0	0	1	0	1
	8.6–12.0	0	0	0	0	0	0	0	0	0	3	2	5
	12.1–15.5	0	0	0	0	0	0	0	1	2	0	1	4
Total		0	0	0	0	0	0	0	1	2	4	3	10
Kanred × Coppei F_3	5.1–8.5	0	0	1	0	0	0	0	0	0	0	0	1
	8.6–12.0	0	1	4	1	8	4	1	1	0	0	0	20
	12.1–15.5	0	0	4	6	15	9	8	3	1	0	0	46
	15.6–19.0	1	0	2	4	7	1	2	0	1	0	0	18
	19.1–22.5	0	0	1	0	0	0	0	0	0	0	0	1
	22.6–26.0	0	0	0	0	1	0	0	0	0	0	0	1
Total		1	1	12	11	31	14	11	4	2	0	0	87

TABLE 4.—*Analysis of variance of F_3 progeny lines of Kanred × Coppei wheat grown in duplicate randomized blocks, Denton, Tex., 1941*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Standard deviation	*F* obtained	*F* required at 5-per-cent level
Blocks	1	0.00406	0.00406		1.424	3.96
Progenies	86	1.0915	.01269		4.452	1.38
Error	86	.24484	.00285	0.053		
Total	173	1.34040				

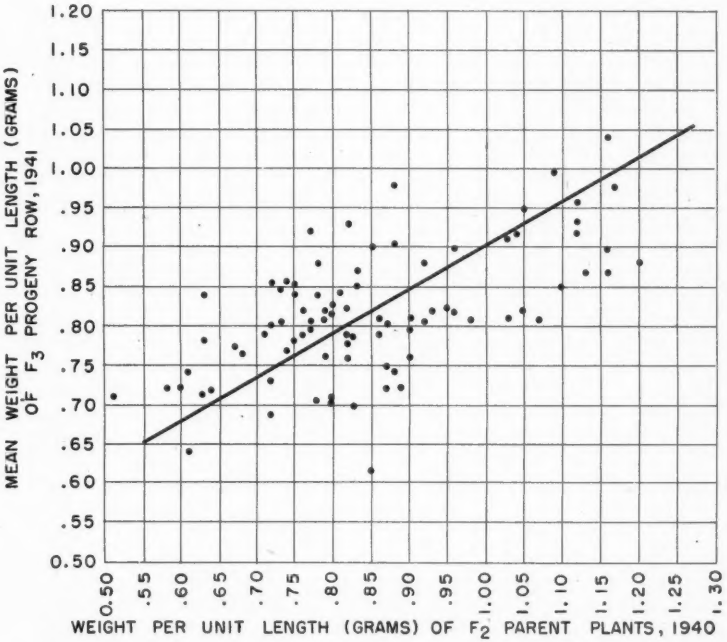

FIGURE 2.—Relation of weights per unit length of Kanred × Coppei F_2 wheat plants grown in 1940 and the means of their F_3 progeny lines grown in 1941, Denton, Tex.

venience. Low temperatures during the winter of 1943 killed all Coppei lines and many hybrid progeny lines as well, so that only 83 could be tested. Of these, both replications were available for only 39 lines.

The analysis of variance for the 39 lines in duplicate plantings is given in table 6. The calculated least significant difference at the 5-percent level was 0.100 gm. per 5-culm sections. The differences between progeny lines were again highly significant.

TABLE 5.—*Frequency distribution for weight per unit length grouped by coefficient-of-variability classes for parental and F_4 progeny lines of the wheat cross Kanred × Coppei, Denton, Tex., 1937 and 1943*

Year and parent or cross	Coefficient-of-variability class	Lines with indicated weight per unit length (grams) per 5-culm sections											Total lines
		0.371–0.420	0.421–0.470	0.471–0.520	0.521–0.570	0.571–0.620	0.621–0.670	0.671–0.720	0.721–0.770	0.771–0.820	0.821–0.870	0.871–0.920	
	Percent	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
1937													
Kanred parent	6. 5–10. 3	0	0	0	1	0	0	0	0	0	0	0	1
	10. 4–14. 1	0	0	0	2	2	1	0	0	0	0	0	5
Total		0	0	0	3	2	1	0	0	0	0	0	6
Coppei parent	6. 5–10. 3	0	0	0	0	0	0	0	0	0	0	2	2
	10. 4–14. 1	0	0	0	0	0	0	0	0	1	0	1	2
	14. 2–17. 9	0	0	0	0	0	0	0	0	1	0	0	1
Total		0	0	0	0	0	0	0	0	2	0	3	5
Kanred × Coppei F_4	6. 5–10. 3	0	0	1	0	2	6	10	4	5	1	0	29
	10. 4–14. 1	0	0	0	1	3	24	18	13	5	1	0	65
	14. 2–17. 9	0	0	0	0	3	2	3	4	1	2	0	15
Total		0	0	1	1	8	32	31	21	11	4	0	109
1943													
Kanred parent	6. 5–10. 3	0	0	0	4	2	0	0	0	0	0	0	6
	10. 4–14. 1	0	0	0	4	3	0	0	0	0	0	0	7
Total		0	0	0	8	5	0	0	0	0	0	0	13
Coppei parent [1]													
Kanred × Coppei F_4	6. 5–10. 3	1	0	0	0	0	0	2	1	1	1	1	7
	10. 4–14. 1	0	1	0	4	7	7	6	3	5	4	3	40
	14. 2–17. 9	0	1	1	4	3	4	3	3	2	0	0	21
	18. 0–21. 7	1	2	1	2	1	0	2	0	0	0	0	9
	21. 8–25. 5	0	1	1	0	0	1	0	0	0	0	0	3
	25. 6–29. 3	0	2	0	0	0	0	0	0	0	0	0	2
	29. 4–33. 1	1	0	0	0	0	0	0	0	0	0	0	1
Total		3	7	3	10	11	12	13	7	8	5	4	83

[1] Winterkilled.

TABLE 6.—*Analysis of variance of F_4 progeny lines of Kanred × Coppei wheat grown in duplicate randomized blocks, Denton, Tex., 1943*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Standard deviation	*F* obtained	*F* required at 5-percent level
Blocks	1	0.019225	0.019225		7.91	4.10
Progenies	38	1.261162	.033188		13.66	1.71
Error	38	.092319	.002429	0.049		
Total	77	1.372706				

The data presented in table 5, although somewhat unsatisfactory because of the small numbers, appear to confirm the conclusions reached from studies of the earlier generations. In 1943, 13 of the 83 hybrid lines had a lower weight per unit length than any of the Kanred lines and 34 had a mean weight per unit length within or below the range of the Kanred parent. This tendency of a larger number of hybrid lines to approach the lodging-susceptible parent occurred in other seasons with other hybrid material. It also was observed in crosses of spring wheat by Waldron (*13*) and by Kilduff (*7*).

The progeny lines of low variability probably are approaching homozygosity for weight per unit length. Of the 31 F_4 progeny lines grown in 1943 from the more uniform F_3 lines, the majority were no more variable than the Kanred parent. The correlation coefficient between weight per unit length of the F_3 plants and their F_4 progeny lines was 0.569. Similar coefficients for all F_4 lines tested in 1937 and 1943 were 0.526 and 0.623, respectively. All three are highly significant statistically and indicate that tests on F_3 plants of hybrid populations should aid in selecting lines of high weight per unit length and probably also for lodging resistance. The relation of weights per unit length of F_3 plants and the means of their F_4 progeny lines grown in 1943 is shown in figure 3.

VARIABILITY AND INHERITANCE OF BREAKING STRENGTH

In 1934, 1936, and 1937 the breaking-strength determinations on all material were made with the Salmon (*10*) machine. When this study was first undertaken the close relation between breaking strength and weight per unit length was unknown. It soon became apparent (*1*, *2*) that the more easily determined measure of weight per unit length could be substituted for breaking-strength tests The close relation between these characters for several hundred varieties that have been studied is indicated by correlation coefficients above 0.90 in each of the three seasons. In F_2 hybrid material grown in 1934 the correlation coefficient between breaking strength and weight per unit length was 0.77, and in 1936 in similar material it was 0.90. Between means of F_3 progeny lines grown in 1936 the correlation coefficient was 0.82. Breaking-strength tests were not made in 1940 or later.

Frequency distributions of breaking strength for Kanred, Coppei, and the F_1 and F_2 populations of the hybrid between these varieties are given in table 7. The number of parent and F_1 plants tested was not adequate for accurate comparisons.

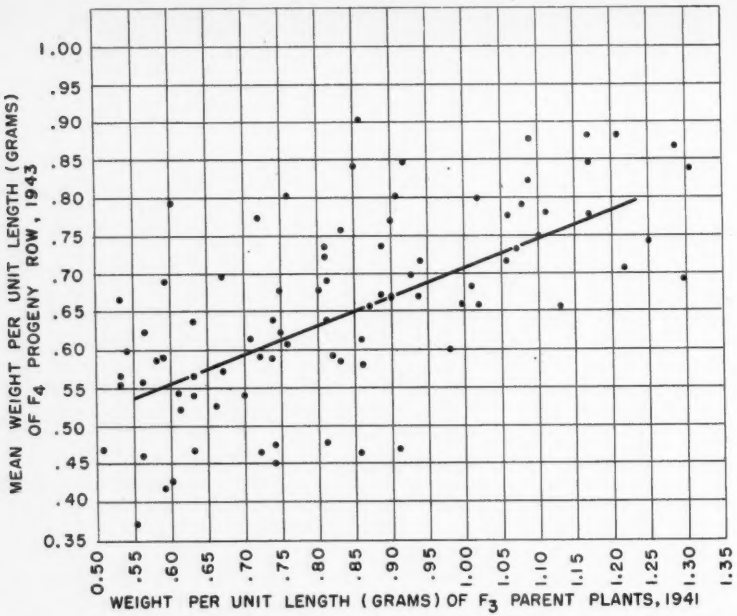

FIGURE 3.—Relation of weights per unit length of Kanred × Coppei F_3 wheat plants grown in 1941 and the means of their F_4 progeny lines grown in 1943, Denton, Tex.

The data presented in table 7 indicate that Kanred and Coppei differ significantly in mean breaking strength. Because the growing season was more favorable, the breaking strength of all material was higher in 1936 than in 1934. In fact, it probably was higher in 1936 than the records indicate for the Coppei parent and some of the hybrids because the machine was not properly adjusted for the higher values as shown by later tests. One result is an unusually large proportion of the population in the upper classes and an abnormally low standard deviation in 1936 as compared with other seasons and with the Kanred parent. This error was not discovered until the tests had been completed.

Breaking-strength tests also were made on the parents and on 153 F_3 progeny lines in 1936. Twenty plants were tested from each line, but only 25 spaced plants in single rows of Kanred and Coppei were tested. The study was continued on the F_4 generation in 1937, when 109 progeny lines were grown. Included in this group were the extremes in breaking strength of the F_3 lines. Others were selected at random. For comparison 9 progeny rows of Kanred and 5 of Coppei were grown. Frequency distributions for the means of F_3 progeny lines in 1936 and for the F_4 lines grown in 1937, together with those of the parental lines, are given in table 8. Since these progeny lines were not replicated, a generalized error could not be calculated and the breaking-strength and coefficient-of-variability classes in table 8 are merely arbitrary intervals.

TABLE 7.—*Frequency distribution for breaking strength of plants of parents and F_1 and F_2 populations of the wheat cross Kanred × Coppei, Denton, Tex., 1934 and 1936*

Year and parent or cross	Plants with indicated breaking strength (pounds) per 5 culms										Total plants	Mean	Standard deviation	Coefficient of variability
	3.51–4.00	4.01–4.50	4.51–5.00	5.01–5.50	5.51–6.00	6.01–6.50	6.51–7.00	7.01–7.50	7.51–8.00	8.01–8.50				
1934	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Pounds*	*Pound*	*Percent*
Kanred parent	3	5	7	3	3	0	0	0	0	0	21	4.85	0.785	16.19
Coppei parent	0	0	0	0	1	4	2	3	10	0	20	7.27	.771	10.61
Kanred × Coppei F_1	0	0	2	3	7	5	3	4	2	0	26	6.25	.832	13.31
Kanred × Coppei F_2	1	4	8	11	15	31	31	33	35	4	173	6.67	.988	14.82
1936														
Kanred parent	0	1	0	0	2	13	8	1	0	0	25	6.37	.553	8.68
Coppei parent	0	0	0	0	0	0	0	0	8	13	21	8.03	.109	1.35
Kanred × Coppei F_1	0	0	0	0	0	0	0	0	0	5	5	8.08	.029	.34
Kanred × Coppei F_2	0	0	0	8	12	18	22	27	64	34	185	7.23	.841	11.63

TABLE 8.—*Frequency distribution for breaking strength grouped by arbitrary coefficient-of-variability classes for means of parental and F_3 and F_4 progeny lines of the wheat cross Kanred × Coppei, Denton, Tex., 1936 and 1937*

Year and parent or cross	Coefficient-of-variability class	Lines with indicated breaking strength (pounds) per 5 culms								Total lines
		4.51–5.00	5.01–5.50	5.51–6.00	6.01–6.50	6.51–7.00	7.01–7.50	7.51–8.00	8.01–8.50	
1936	*Percent*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Kanred parent	7.1–10.0	0	0	0	1	0	0	0	0	1
Coppei parent	1.1–4.0	0	0	0	0	0	0	0	1	1
Kanred × Coppei F_3	1.1–4.0	0	0	0	0	0	0	3	1	4
	4.1–7.0	0	0	0	0	0	0	9	0	9
	7.1–10.0	0	0	0	0	1	16	14	0	31
	10.1–13.0	0	0	0	4	20	30	4	0	58
	13.1–16.0	0	0	0	8	20	7	0	0	35
	16.1–19.0	0	0	1	3	6	0	0	0	10
	19.1–22.0	0	1	2	3	0	0	0	0	6
Total		0	1	3	18	47	53	30	1	153
1937										
Kanred parent	7.1–10.0	1	1	0	0	0	0	0	0	2
	10.1–13.0	1	3	0	0	0	0	0	0	4
	13.1–16.0	2	0	1	0	0	0	0	0	3
Total		4	4	1	0	0	0	0	0	9
Coppei parent	7.1–10.0	0	0	0	0	0	3	0	0	3
	10.1–13.0	0	0	0	0	0	1	0	0	1
	13.1–16.0	0	0	0	0	1	0	0	0	1
Total		0	0	0	0	1	4	0	0	5
Kanred × Coppei F_4	7.1–10.0	0	0	4	5	7	1	0	0	17
	10.1–13.0	1	4	19	11	9	1	1	0	46
	13.1–16.0	2	4	17	14	3	0	0	0	40
	16.1–19.0	0	0	3	1	1	0	0	0	5
	19.1–22.0	0	0	0	0	0	1	0	0	1
Total		3	8	43	31	20	3	1	0	109

The F_3 progeny lines showed the same abnormal accumulation at the upper limit of the range of the breaking-strength machine as previously noted. Progeny lines having high breaking strength were in the lower classes of coefficient of variability and those having low breaking strength were in the upper classes of variability. The F_4 progeny lines ranged from the lower limits of the Kanred parent to one line having mean breaking strength greater than any Coppei parent line tested. The data indicate that in the F_4 lines there was no close relation between breaking-strength means and their coefficient-of-variability classes.

The correlation coefficient between breaking strength of F_2 parent plants grown in 1934 and means of their F_3 progeny lines grown in 1936 was 0.342 and that between F_3 parent plants of 1936 and means of their F_4 progeny lines grown in 1937 was 0.404. Although both figures are statistically significant, they are not sufficiently high to be of great value in selecting plants that would maintain high breaking strength in later generations. Smith (*11*) after a study of hybrid progenies in an oat cross came to a similar conclusion.

VARIABILITY AND INHERITANCE OF OTHER MORPHOLOGICAL CHARACTERS MEASURED

The characters total weight of culm, weight of head, diameter of culm, length of lower internode, and length of head were also measured.

Since previous studies of these characters in wheat varieties by Atkins (*1*, *2*) showed them to be less closely correlated with field lodging than are breaking strength or weight per unit length, the data are not reported in detail here. The means of the parents were significantly different statistically for each of these characters. Inheritance appeared to be controlled by multiple factors, resulting in the recovery of widely differing F_3 and F_4 progeny lines. Correlation coefficients between measurements of F_2 plants and the means of their F_3 progeny lines were 0.582 for diameter of culm, 0.694 for plant height, and 0.830 for head length, indicating that desired types of these characters can be selected with considerable success in the F_2 generation. Similar correlations for total weight of culm, weight of head, and length of lower internode were low. These results are in agreement with previous results obtained in studies of wheat varieties by Atkins (*1*) and in oats by Smith (*11*).

The inheritance of several spike characters, namely, density, length, awn development, and glume pubescence, also was studied with reference to their relation to weight per unit length. Since the inheritance of these spike characters has been studied by others, the detailed data for the present cross are not reported. The inheritance of awns was controlled by a single factor with incomplete dominance of the awnless condition in the F_1 generation. Pubescence of glumes was dominant and controlled by a single factor. One major factor controlled the inheritance of head type; but modifying factors were present, resulting in transgressive segregation for head length and the production of F_4 lines varying in head type and length from extremely short heads of the club type to heads of greater length than those of the Kanred parent.

INTERRELATION OF ALL CHARACTERS MEASURED

The interrelation of all characters measured was determined by means of correlation coefficients as shown in table 9. A study of the correlation coefficients in parental and hybrid populations indicates that many of these characters are associated to some extent. Weight per unit length was significantly correlated with total weight of culm and diameter of culm ($r=0.55$ to 0.83). In the Kanred parent the correlation coefficient between weight per unit length and plant height was 0.57, while in the Coppei parent it was only 0.02 and for all hybrid material it was low. In the Coppei parent weight per unit length was significantly correlated with length of lower internode ($r=0.62$), but in all other material similar correlations were nonsignificant.

Total weight of culm was most closely correlated with weight per unit length and with weight of heads. Diameter of culm was most closely correlated with weight per unit length, with weight of culm, and in the F_3 population with weight of heads. Plant height was significantly correlated in the F_2 and F_3 populations with length of head ($r=0.55$ to 0.64). Length of lower internode was independent of most other characters except in the F_3 population in which it was correlated with other characters to a moderate degree. Weight of head was most closely associated with weight per unit length, weight of culm, and diameter of culm. Length of head showed relatively low correlations with other characters except for plant height in the F_2 and F_3 populations.

TABLE 9.—*Correlation coefficients (r) for various plant characters of Kanred, Coppei, and Kanred × Coppei wheats, Denton, Tex., 1940 and 1941*

Year, parent or cross, and character correlated with character indicated in box	Basis	Weight of 5 culms (gm.)	Diameter of 5 culms (mm.)	Plant height (cm.)	Length of lower internode (cm.)	Weight of 5 heads (gm.)	Head length (cm.)
1940							
Kanred parent:							
Weight per unit length (gm.)	200 plants [1]	0.67	0.60	0.57	0.07	0.42	0.03
Weight of 5 culms (gm.)		------	.57	.68	.05	.57	.45
Diameter of 5 culms (mm.)		------	------	.43	−.05	.32	.26
Plant height (cm.)		------	------	------	.02	.46	.29
Length of lower internode (cm.)		------	------	------	------	.01	.08
Weight of 5 heads (gm.)		------	------	------	------	------	.40
Head length (cm.)		------	------	------	------	------	------
Coppei parent:							
Weight per unit length (gm.)	do [1]	.64	.64	.02	.62	.59	.38
Weight of 5 culms (gm.)		------	.59	.42	.03	.56	.17
Diameter of 5 culms (mm.)		------	------	.26	.00	.47	.26
Plant height (cm.)		------	------	------	.16	.03	.16
Length of lower internode (cm.)		------	------	------	------	.04	−.01
Weight of 5 heads (gm.)		------	------	------	------	------	.44
Head length (cm.)		------	------	------	------	------	------
Kanred × Coppei F_2:							
Weight per unit length (gm.)	480 plants [2]	.55	.63	.21	.03	.46	.18
Weight of 5 culms (gm.)		------	.62	.35	.08	.48	.21
Diameter of 5 culms (mm.)		------	------	.07	−.01	.42	.13
Plant height (cm.)		------	------	------	.21	.26	.55
Length of lower internode (cm.)		------	------	------	------	.01	.11
Weight of 5 heads (gm.)		------	------	------	------	------	.20
Head length (cm.)		------	------	------	------	------	------
1941							
Kanred × Coppei F_3:							
Weight per unit length (gm.)	87 progeny lines. [3]	.78	.83	.34	.27	.64	.33
Weight of 5 culms (gm.)		------	.79	.58	.38	.69	.31
Diameter of 5 culms (mm.)		------	------	.37	.44	.68	.39
Plant height (cm.)		------	------	------	.49	.51	.64
Length of lower internode (cm.)		------	------	------	------	.40	.25
Weight of 5 heads (gm.)		------	------	------	------	------	.23
Head length (cm.)		------	------	------	------	------	------

[1] 5-percent level of significance, 0.138; 1-percent level, 0.181.
[2] 5-percent level of significance, 0.088; 1-percent level, 0.115.
[3] 5-percent level of significance, 0.205; 1-percent level, 0.267.

CONTINGENCY STUDIES

The segregation of spike characters was recorded in the F_2 and F_3 populations. If any of these characters should be linked with genes determining lodging resistance as indicated by weight per unit length, then they might be useful as an aid in selecting plants in early generations. To determine the relation of these characters to weight per unit length, χ^2 tests for independence between weight per unit length and the spike characters pubescence of glumes, awn type, and head type and length were made for the 1940 F_2 data. In preparing contingency tables, no class division that had a lower expectancy than 6 was used. Results of the tests are given in table 10.

Pubescence of glumes, head type, and head length were independent of weight per unit length. Awn type was not entirely independent as a slightly larger proportion of awnless plants were in the higher weight-per-unit-length classes. However, the association was not high and awned types of relatively high weight per unit length were recovered. A similar relation was observed by Clark, Florell, and Hooker (*4*). In figures 4 and 5 are shown awned and awnless F_4 lines of the club-head and common types having relatively high and low mean weight per unit length. The parent varieties are shown for comparison. Coppei

TABLE 10.—χ^2 *tests for independence of weight per unit length and spike characters in* F_2 *population of the wheat cross Kanred × Coppei, Denton, Tex., 1940*

Spike character	χ^2	Degrees of freedom	*P*
Pubescence of glumes	7.254	4	0.05–0.10
Awn type	8.443	6	.20–.30
Head type	13.542	6	.02–.05
Head length	16.869	6	.01

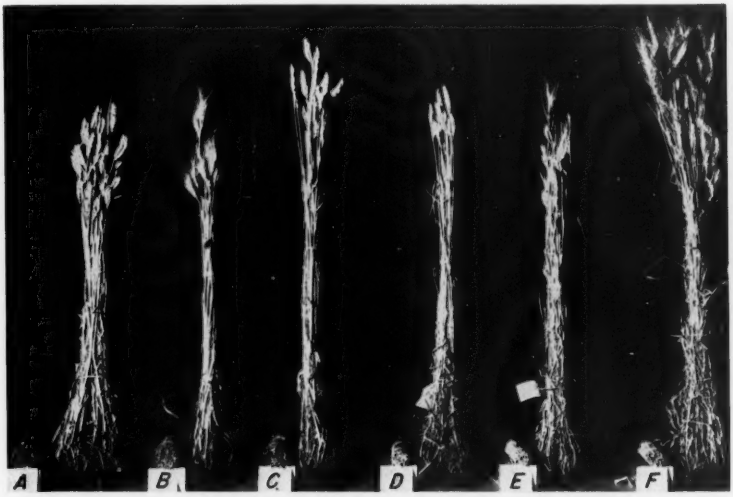

FIGURE 4.—Recovery of F_4 progeny lines of wheat having club heads and mean weight per unit length approaching that of each of the parental progeny lines, 1943: *A*, Coppei parent, 1.066 gm.; *B*, Kanred × Coppei (Sel. 73–350–18), 0.882 gm.; *C*, Kanred × Coppei (Sel. 73–183–10), 0.845 gm.; *D*, Kanred × Coppei (Sel. 73–141–17), 0.417 gm.; *E*, Kanred × Coppei (Sel. 73–390–31), 0.469 gm.; *F*, Kanred parent, 0.567 gm. The bundle of 100 culm sections at the base and left of each plant shows the relative size of culm of each progeny line.

progeny lines were winterkilled in 1943, but a few plants that survived in the rows are shown. Data for Coppei in 1941 were substituted for 1943, since none were available for 1943. As pointed out previously, no F_3 or F_4 progeny lines of extremely high weight per unit length were recovered, although some approached the Coppei lines. Progeny lines having mean weight per unit length within and below the range of the Kanred parent were recovered.

SUMMARY

Weight-per-unit-length measurements have been used successfully at Texas Substation No. 6, Denton, Tex., and several other agricultural experiment stations in the Midwest to evaluate varieties and strains of winter wheat for resistance to lodging. In the present study such tests were used on hybrid populations of a cross between the lodging-

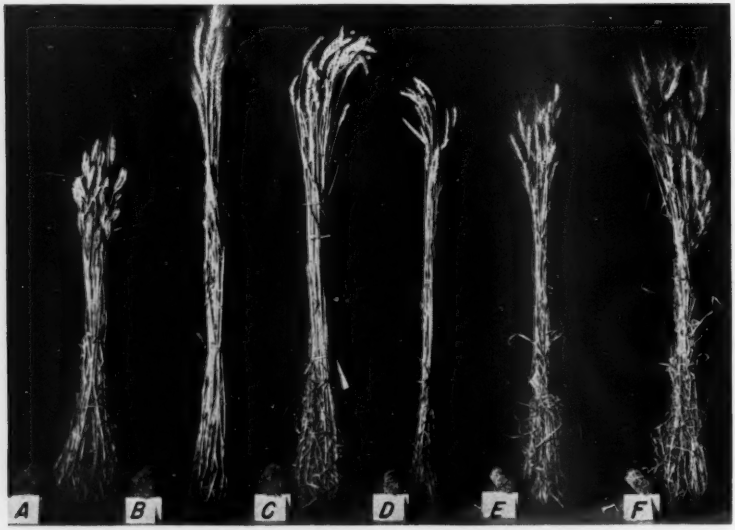

FIGURE 5.—Recovery of F_4 progeny lines of wheat having heads of the common type and mean weight per unit length approaching that of each of the parental progeny lines, 1943: *A*, Coppei parent, 1.066 gm.; *B*, Kanred × Coppei (Sel. 73–30–40), 0.883 gm.; *C*, Kanred × Coppei (Sel. 73–352–7), 0.887 gm.; *D*, Kanred × Coppei (Sel. 73–113–3), 0.464 gm.; *E*, Kanred × Coppei (Sel. 73–458–12), 0.370 gm.; *F*, Kanred parent, 0.567 gm. The bundle of 100 culm sections at the base and left of each plant shows the relative size of culm of each progeny line.

resistant club wheat variety, Coppei, and the lodging-susceptible common wheat variety, Kanred, to determine whether such tests can be made on individual plants in the early generations of a hybrid to select plants having high weight per unit length and the ability to transmit this characteristic to their progeny.

Tests conducted in several seasons on F_2, F_3, and F_4 populations and parental varieties of the cross indicate that environmental influences are large. This is shown by the range and variability of parents and F_1 plants, in which no genetic variability would be expected. The correlation coefficient between weight per unit length in F_2 parent plants and the means of their F_3 progeny lines was 0.609 in 1941. The similar correlation coefficient for the F_3 parent plants and their F_4 progeny lines in 1943 was 0.623. These coefficients indicate that the method may be used to select plants of high weight per unit length that will transmit this characteristic to their progeny. As no lodging occurred during the period of this experiment, the relation of weight per unit length in these hybrid lines to field lodging could not be determined.

Correlation coefficients of F_2 parent plants and their F_3 progeny lines were 0.582 for diameter of culm, 0.694 for plant height, and 0.830 for length of head. These correlation coefficients indicate, as with weight per unit length, that selection for these characters can be

made in early generations and that continued selection will lead to the desired type. Correlation coefficients between F_2 parent plants and their F_3 progeny lines for weight of heads, length of lower internode, and weight of culms were low or nonsignificant.

The inheritance of awns was controlled by a single-factor pair, with incomplete dominance of the awnless character. There was a low association between awnless head type and the higher weight-per-unit-length classes. Pubescence of glumes was dominant in the F_1 and controlled by a single factor. It was independent of weight per unit length. One major-factor pair controlled the inheritance of head type; but transgressive segregation for head length, with the production of homozygous intermediate and extreme types, was observed in the F_3 and F_4 populations. Therefore it is assumed that complementary factors were present. Head length was independent of weight per unit length.

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